British Dinantian (Lower Carboniferous) Terebratulid Brachiopods

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Synopsis

Six genera of terebratulid brachiopods are recognized in the British Dinantian rocks; their principal characteristics, especially the dispositions of their hinge plates, are described to allow recognition. The name *Dielasma hastata* (J. de C. Sowerby), of much previous literature, is shown to include several species and the true *hastata* is redescribed within the genus *Beecheria*. The new species *Harttella oakleyi* is described.

Introduction

In Britain, and indeed most of Europe, Carboniferous terebratulids have received little attention taxonomically, and have never been reviewed. This study arose from, and extends beyond, the investigations into four taxa found in the acid-developed silicified faunas of County Fermanagh, Ireland (see Brunton 1966, 1968). These four terebratulids are described in detail elsewhere (in preparation), but investigations of their taxonomic positions made it clear that many more terebratulids are to be found in Britain than one would think from the literature.

Silurian and Devonian terebratulids have been described by Cloud (1942) and Permian taxa by Campbell (1965) and Stehli (1956, 1961, 1965). However, in Britain the literature abounds with references to *Dielasma hastata* (J. de C. Sowerby), but little else. *Alwynia* was described by Stehli (1961), based upon *Terebratula vesicularis* de Koninck, which is recorded from the Isle of Man, and the species *Terebratula sacculus* J. de C. Sowerby has been placed by some authors in *Girtyella* (e.g. Muir-Wood 1951).

Terebratulids present serious difficulties to the taxonomist because many taxa resemble each other externally, whilst having distinctive internal morphologies. Particularly in the Mesozoic this problem has been attacked by serially sectioning specimens in attempts to see or reconstruct their internal morphologies. The sectioning of Lower Carboniferous specimens, plus information from silicified material, allows the easy recognition of six genera of terebratulids. In addition the necessary computing facilities have become available which allow a series of drawings of serial sections to be entered to a computer programmed to provide drawings, or screen display, of the specimen viewed from any direction and as if restored to three dimensions. Stereo-pairs of these drawings allow viewing with a three-dimensional effect (Fig. 20, p. 55). This technique allows accurate drawings of the shell interior to be reproduced easily, whereas in the past complex drafting techniques, or sheer guesswork, were used.

Palaeozoic terebratulids were described by Stehli in the *Treatise* (1965), with the emphasis of classification being upon the length of the loop, which in life supported the lophophore. In the introduction to the Terebratellidina Muir-Wood & Stehli wrote in the *Treatise* (Stehli 1965 : H730): 'For the Terebratulida as a whole, we still lack essential information concerning internal characters, especially of the Triassic genera, and consequently it is not now possible to shape a sound classification or to give a satisfactory outline of evolution.' Dagys accepted this challenge and in 1972 published a reclassification of terebratulids, based

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largely upon his experience of Triassic species. Dagys was less concerned with loop length than with the form and ontogeny of the cardinalia as a whole. In particular the development and dispositions of the hinge plates in dorsal valves are important in characterizing genera and suprageneric groups. Of the seven superfamilies Dagys (1972) recognized within the Terebratulida, two are represented in the Carboniferous of Europe by the following genera:

Cryptonellacea	Dielasmatacea
Cryptonellidae	Dielasmatidae
Cryptonella	*Dielasma?*
Cranaenidae	*Balanoconcha*
Girtyella	Heterelasminidae
Harttella	*Beecheria*
Notothyridae	
Alwynia	

In these Carboniferous genera, those which in adulthood have entire hinge plates free of the valve floor (other than for connections to a median septum) fall into the Cryptonellacea, while the dielasmatacean genera have hinge plates joining to the valve floor medially and tending to separate anteriorly. Each genus has a distinctive combination of hinge plate dispositions and presence or absence of dental plates (Fig. 1, A–F). Thus a section perpendicular to the long axis of the shell a few mm from the dorsal umbo, and a check on the ventral umbo for dental plates, allows generic assignment. The presence of true *Dielasma* in the British Carboniferous is now in doubt and the genus is not described here.

Specific differences are to be found externally in the shell form and the details of shape of the anterior commissure, internally in details of hinge plate morphology, disposition of the crura and details of the pedicle aperture. When preserved, colour banding is also probably specific, as may be the density of endopuncta within the shell. This last feature has been discussed for fossil terebratulids by Campbell (1965) and for Recent species by Foster (1974). They suggested that ecological conditions dictated endopunctal densities, so that species in

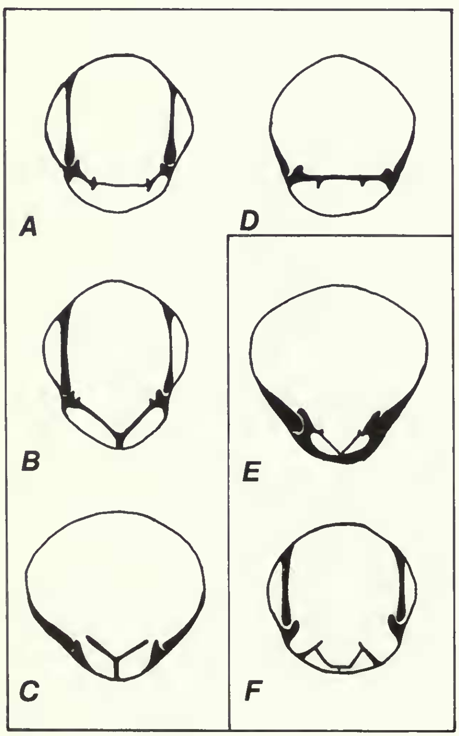


Fig. 1 Transverse sections through the umbonal regions of six Dinantian terebratulid genera. The orientation of the sections is with dorsal valves downwards. Sections A–D, *Cryptonella*, *Girtyella*, *Harttella* and *Alwynia* respectively, belong in the Cryptonellacea, while sections E and F, *Balanoconcha* and *Beecheria*, belong in the Dielasmatacea. The appearance of the dorsal sockets and hinge plates varies according to the positions of the sections. Thus *Harttella* (C) cut nearer the umbo shows hinge plates and socket ridges united in a similar fashion to *Girtyella* (B). *Balanoconcha* (E) cut further from the umbo would show the inner hinge plates separated on the valve floor medially.

warm waters may have more endopunctae per mm² than those in cold water. This, however, cannot be the only answer since four species occurring together in County Fermanagh display a wide variation in endopunctal densities. It seems likely that zoological differences at species level are fundamentally important, but that variations occur intraspecifically which are influenced by ecology. Thus the Fermanagh *Cryptonella* species has high endopunctal densities (at about 450 per mm²) while the other species rate between 100 to 250 per mm².

Systematic palaeontology

In this section each of the six British Carboniferous genera is briefly described and characterized. Under *Beecheria* more information is provided, since this genus is to a large extent replacing the name *Dielasma*.

Synonymy notations are as in Matthews (1973).

Genus *CRYPTONELLA* Hall, 1861

TYPE SPECIES. *Terebratula rectirostra* Hall, 1860, from the mid-Devonian of North America.

REMARKS. The relatively long-looped cryptonellids are seldom recorded from the Carboniferous of Europe and in general *Cryptonella* itself is similar externally to genera like *Cranaena* or *Dielasma*. The loops in terebratulids are commonly broken so *Cryptonella* must be recognized by other means. One characteristic is that the ventral umbo of *Cryptonella* species is nearly straight to suberect in position, and so leaves the deltidial plates exposed (Fig. 2), in contrast to the more strongly incurved beaks of most other genera. In

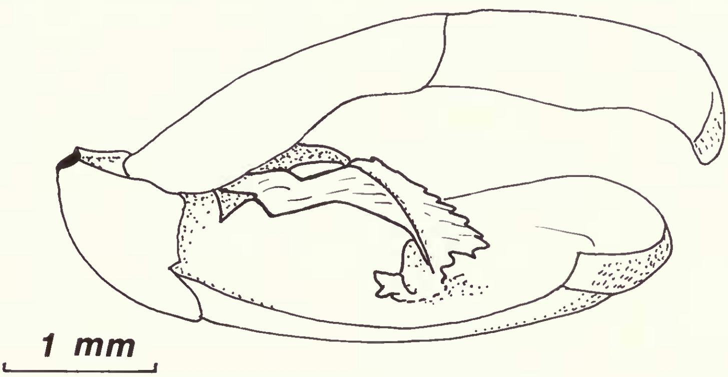


Fig. 2 Drawing of a lateral view of a silicified juvenile specimen of *Cryptonella* sp. from Co. Fermanagh, Ireland, showing the almost straight ventral umbo and immature (cryptacanthiiform) loop, the ventral tip of which, in this specimen, is cemented by siliceous deposits to the ventral valve.

addition the endopunctation of Carboniferous *Cryptonella* is fine and very abundant, there being approximately 450 endopuncta per mm², more than twice the density of other Carboniferous genera. Internally, the disposition of the hinge plates resembles that of *Alwynia*, but the latter has no dental plates. In detail the hinge plate is perforated posteriorly and remains unsupported between the inner socket ridges. The crural bases, which are close to the socket ridges, form ridges on both the dorsal and ventral surfaces of the hinge plate. Dental plates are usually well developed (Fig. 3). *Cryptonella* species in the British Dinantian resemble some *Girtyella* species and, other than by endopunctation, the two groups are best differentiated by their internal morphologies.

Amongst the many terebratulids described by de Koninck (1887), two externally resemble

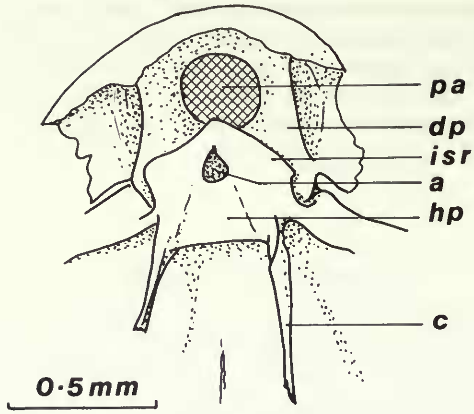


Fig. 3 Drawing of the internal posterior region of a silicified *Cryptonella* sp. from Ireland. The ventral umbo, with its pedicle aperture (pa) and dental plates (dp), is uppermost. The aperture (a) at the posterior end of the hinge plate (hp) leads to the cavity below the hinge plate. Indistinct outer hinge plates connect the inner socket ridges (isr) to the crural bases, from which the crura (c) extend anteriorly.

Cryptonella and may belong here; they are *Dielasma amygdaloides* (1887 : pl. 4, figs 26–40) and *D. subfusiforme* (1887 : pl. 5, figs 32–44).

Cryptonellid genera have been described in detail from the Permian of SW Texas by Cooper & Grant (1976).

Genus *GIRTYELLA* Weller, 1911

TYPE SPECIES. *Hattinia indianensis* Girty, 1908, from the Pella beds of Iowa, correlated with the late Meramec Ste Geneviève limestones, considered to be of late Asbian age.

REMARKS. It should be noted that the *Treatise* illustration (Stehli 1965 : fig. 614.2b) of the genus is poor in that the inner hinge plates should be concave onto the low median septum, forming a distinct Y-shaped structure in cross section (Fig. 1B), as originally illustrated by Weller (1911). *Girtyella* resembles the Permian genus *Fletcherithyris* Campbell internally,

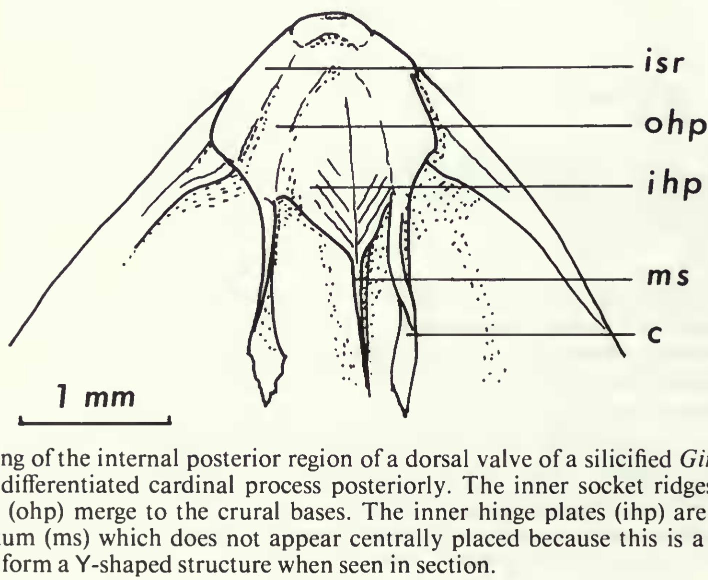


Fig. 4 Drawing of the internal posterior region of a dorsal valve of a silicified *Girtyella* sp. There is a weakly differentiated cardinal process posteriorly. The inner socket ridges (isr) and outer hinge plates (ohp) merge to the crural bases. The inner hinge plates (ihp) are supported on a median septum (ms) which does not appear centrally placed because this is a slightly oblique view. These form a Y-shaped structure when seen in section.

but the former has a persistent median septum while in the Permian genus it only raised the inner hinge plates off the valve floor late in ontogeny. In addition the endopunctal density is very low in *Fletcherithyris*, being less than half the 250 or so per mm² expected in *Girtyella*.

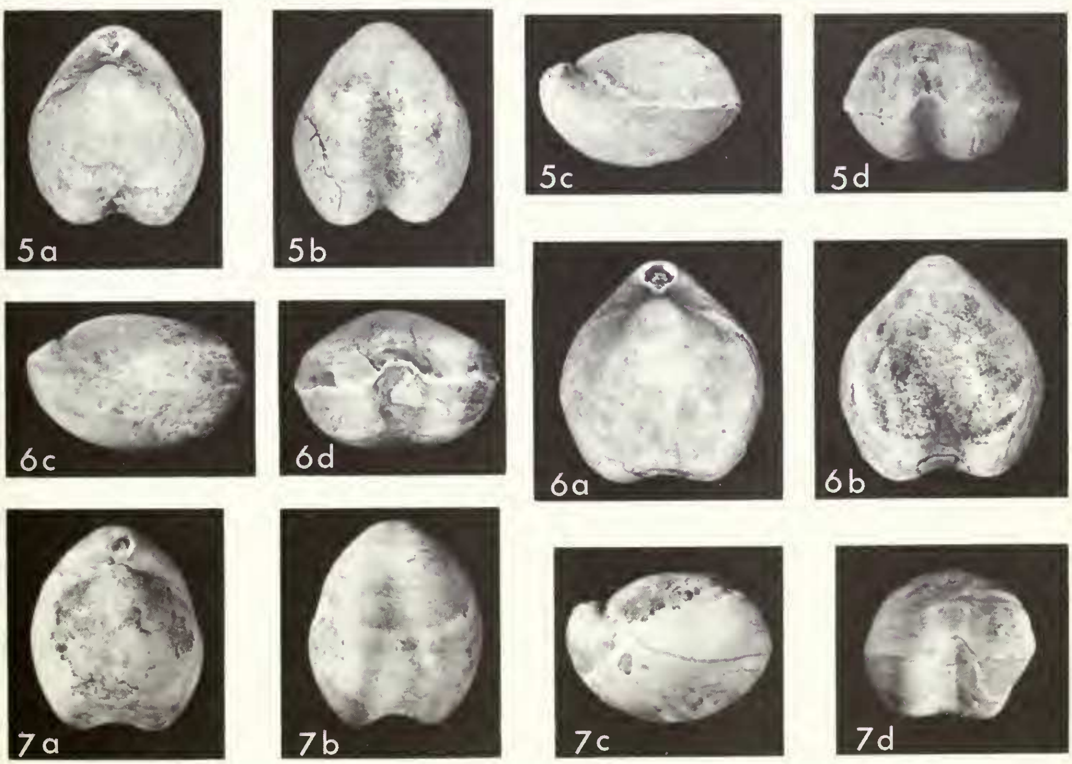
Girtyella species are small to medium-sized, they tend to be fat, i.e. broad and strongly biconvex, and commonly have late stage sulci in their valves. Internally the ventral valve has dental plates, although they may be short, and the hinge plates form a Y-shaped structure by fusion with the persistent median septum. The crural bases are close to the inner socket ridges and can be traced on the ventral surface of the hinge plates (Fig. 4).

Muir-Wood (1951) suggested that *Terebratula sacculus* J. de C. Sowerby belonged to this genus. However, inspection of the lectotype and other specimens leads me to believe that it should be assigned to *Balanoconcha* Campbell (see p. 52).

Genus *HARTTELLA* Bell, 1929

TYPE SPECIES. *H. parva* Bell, 1929, from the Lower Windsor Group (Zone B of Bell), Nova Scotia, Canada. On micropalaeontological evidence Jansa, Mamet & Roux (1978) correlate these beds with late Viséan strata of western Europe.

REMARKS. This genus, not previously recognized in Europe, is small, commonly no more than 10 mm long, either smooth or with a deep ventral valve sulcus, especially anteriorly. Internally the genus lacks dental plates and the hinge plates fuse medially onto a median septum, forming a Y-shaped structure (Fig. 1C), as in *Girtyella*.



Figs 5–7 *Harttella oakleyi* sp. nov. Fig. 5a–d, **holotype** viewed dorsally, ventrally, laterally and anteriorly; from the collection of K. P. Oakley and C. D. Ovey from near Ashover, Derbyshire; of late Viséan, Brigantian, age. BM(NH) Pal. Dept. no. BD 68, ×3. Fig. 6a–d, paratype viewed dorsally, ventrally, laterally and anteriorly; from the above collection. BM(NH) no. BD 69, ×3. Fig. 7a–d, the specimen illustrated by J. de C. Sowerby (1824 : pl. 446, fig. 1 top left) as *Terebratula sacculus*, from Derbyshire. BM(NH) no. B 61654, ×2·5.

In describing *T. sacculus*, J. de C. Sowerby (1824 : pl. 446, fig. 1 top left) illustrated a specimen which is, in fact, a *Harttella* species (Figs 7a–d). Other examples of the genus in the BM(NH) collections include those described below as *H. oakleyi* sp. nov., and about thirty congeneric specimens collected by the author from near Middleton in Teesdale.

The type species, *H. parva*, lacks folding, but another Windsor Group species, *H. gibbosa* Bell, from beds approximately equivalent to the late Viséan of Europe, is sulcate in a similar fashion to the new British species.

Harttella oakleyi sp. nov.
Figs 5–7

v. 1824 *Terebratula sacculus* J. de C. Sowerby: 65; pl. 446, fig. 1 top left.

DIAGNOSIS. *Harttella* with strong, persistant ventral valve sulcus and uniplicate commissural fold.

DESCRIPTION. Small (up to 10 mm long) shells with prominent, erect, ventral umbo. Strongly biconvex lateral profile with opposed growth anteriorly in adulthood. Ventral valve with increasingly deep sulcus developed from about 4 mm from umbo and forming narrow uniplicate fold in anterior commissure and ligate outline. Hinge plates raised on high median septum anteriorly and crural bases springing from their ventral surfaces.

NAME. The type specimens are named after the late Dr Kenneth P. Oakley, of the British Museum (Natural History), who collected them in 1946.

HOLOTYPE. BM(NH) Palaeont. Dept. no. BD 68, collected by K. P. Oakley and C. D. Ovey from Fall Hill quarry, Milltown, near Ashover, Derbyshire, from late Viséan (Brigantian) limestones. Fig. 5a–d.

MATERIAL. Approximately fifty other specimens from the Oakley & Ovey collection, nos BD 69–BD 79. A single specimen in the Sowerby Collection, figured by J. de C. Sowerby (1824), B 61650, and probably collected between Matlock and Derby.

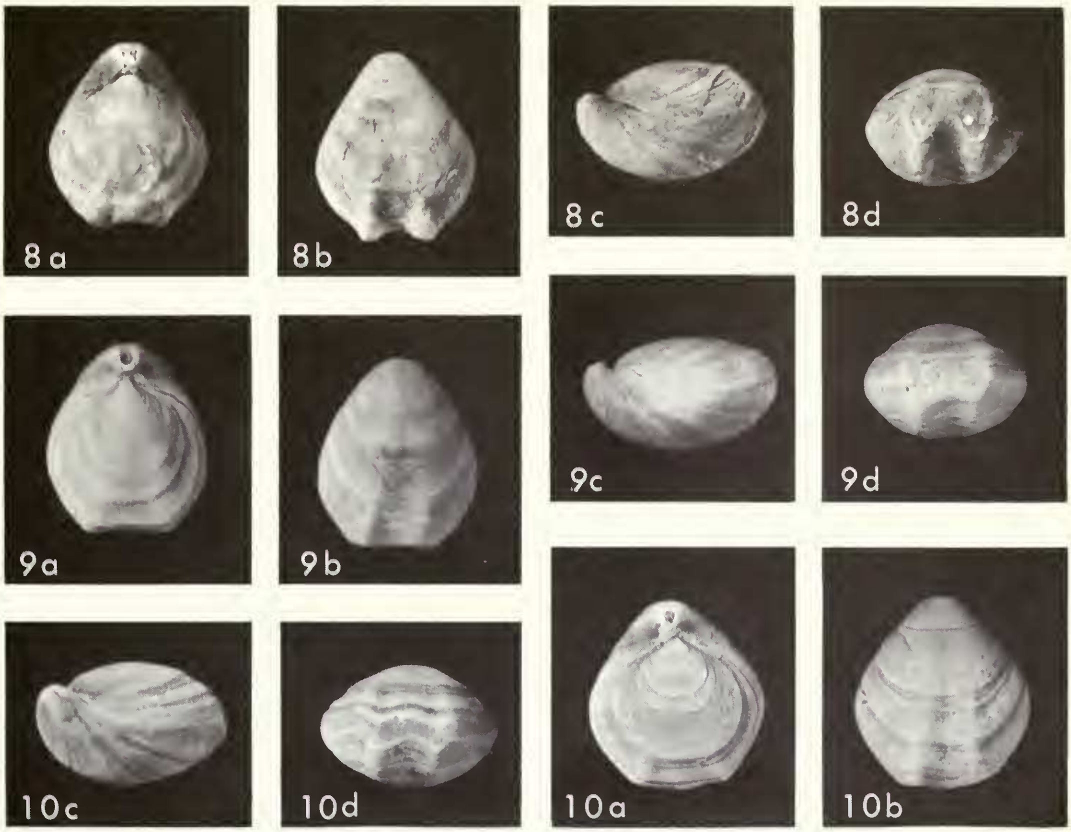
REMARKS. *H. oakleyi* externally somewhat resembles *B. saccula*, to which it has normally been attributed in the past, but differs in being smaller (adults being less than half the length of *B. saccula*) and in having a much more strongly developed sulcus in the ventral valve. In *B. saccula* the ventral sulcus developed late in ontogeny and the dorsal valve commonly remained only slightly affected at the commissure. In contrast the ventral sulcus of *H. oakleyi* started within about 4 mm of the ventral umbo (i.e. at less than half the adult shell length) and persisted, with increasing width and depth, to the ligate anterior margin where the commissure is sharply uniplicate (Figs 5–7, b, d). In some specimens the ligate nature of the anterior margin is accentuated by an anteriorly developed groove on the dorsal valve. Internally, the dispositions of the hinge plates in these two species are quite different (Fig. 1C, E). The species differs from *H. gibbosa* Bell in having a ventral sulcus originating close to the umbo; in Bell's species the sulcus is restricted anteriorly. Judged on Bell's serial sections (1929 : 151), the dorsal valve is more heavily thickened around the sockets than in the British species.

At present *H. oakleyi* is known only from late Viséan limestones in Derbyshire, but closely related specimens are known from the early Namurian of Yorkshire.

Genus *ALWYNIA* Stehli, 1961

TYPE SPECIES. *Terebratula vesicularis* de Koninck, 1851, a rare species from the Visé district of Belgium, probably of mid to late Viséan age.

LECTOTYPE. Here selected, specimen in the de Koninck Collection of the British Museum (Natural History) Palaeont. Dept., no. BD 80, from the Visé region of Belgium. None of the ten de Koninck specimens looks like the original 1851 figuring, but the chosen specimen matches closely to that later figured by de Koninck (1887 : pl. 8, figs 30–33) and is illustrated here (Fig. 8a–d).



Figs 8–10 *Alwynia vesicularis* (de Koninck). Fig. 8a–d, **lectotype** viewed dorsally, ventrally, laterally and anteriorly; from de Koninck's collection from the Visé region of Belgium; of mid to late Viséan age. BM(NH) Pal. Dept. no. BD 80, ×2·5. Fig. 9a–d, a second specimen from de Koninck's collection, viewed dorsally, ventrally, laterally and anteriorly. BM(NH) no. BD 86, ×2. Fig. 10a–d, a third specimen from the same collection, viewed dorsally, ventrally, laterally and anteriorly. BM(NH) no. BD 85, ×2.

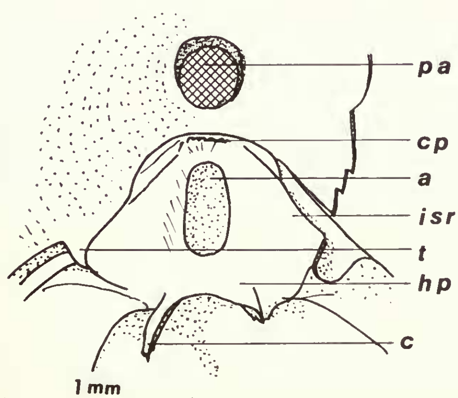


Fig. 11 Drawing of the interior posterior region of a silicified *Alwynia* specimen from Ireland. The ventral valve is uppermost and has a thickened rim to the pedicle aperture (pa). The dorsal valve has a weakly developed cardinal process (cp), a large aperture (a) in the hinge plate (hp) and crural bases forming ridges on the underside (dorsal surface) of the hinge plate. The crus (c) on the right, as well as the anterior end of the socket, is broken.

REMARKS. Stehli (1961) included only the type species in the genus, although a second species is now known from Ireland. These are small, relatively deep-bodied species with anteriorly developed opposite or alternate folding. In *A. vesicularis* this forms a characteristic antiplicate anterior commissure (Fig. 8d), while in the Irish species the commissure is rectimarginate but with a ligate anterior margin. *Alwynia* species resemble *T. sacculus*, but internally the two differ considerably. *Alwynia* has no dental plates and the hinge plates form a horizontal, medially unsupported, structure with the crural bases forming ridges on its dorsal surface (Fig. 11).

Specimens from the type locality, Visé, are likely to be of Asbian age, as are those specimens of *A. vesicularis* known from the Isle of Man. The Irish species is also of Asbian age.

Genus *BALANOCONCHA* Campbell, 1957

TYPE SPECIES. *B. elliptica* Campbell, 1957, from the Watts district of New South Wales, Australia. When first described the age of these beds was thought to be Tournaisian, but recent work has assigned them to a mid to upper Viséan age (Roberts 1975).

REMARKS. This Australian Viséan genus was discovered when trying to assign *T. sacculus* J. de C. Sowerby to a modern genus, having realised that it could not be included in *Girtyella*. *Balanoconcha* is characterized by having no dental plates in the ventral valve and inner hinge plates which fuse to the dorsal valve floor medially forming a V-shaped structure posteriorly (Fig. 1E), but separating anteriorly, as in *Dielasma* (which has dental plates).

When selecting the lectotype of *T. sacculus* (Fig. 14), Muir-Wood (1951) thought the specimen contained a single dental plate. This piece of shell is, I think, not a dental plate but a shelly fragment trapped in the ventral umbo. Several other specimens, matching the type externally, were sectioned and all display the internal structures characteristic of *Balanoconcha*.

Externally *Balanoconcha* resembles *Alwynia* in being somewhat rounded with anterior

Figs 12–14 *Balanoconcha saccula* (J. de C. Sowerby). Fig. 12a–c, ventral, dorsal and anterior (note, ventral valve upper) views of a specimen from Narrowdale, near Alstonfield, Staffordshire. BM(NH) Pal. Dept. no. B 49340, ×1·5. Fig. 13a–c, dorsal, ventral and lateral views of a specimen from the same locality which, when young, was severely damaged (arrowed) and grew asymmetrically with scar tissue on both valves. BM(NH) no. B 49341, ×1·5. Fig. 14a, b, lectotype (sel. Muir-Wood, 1951), viewed dorsally (showing the median septum, arrowed) and anteriorly (ventral valve uppermost), from the Sowerby collection. BM(NH) no. B 61653, ×1·5.

folding. Most of the specimens up to lengths of about 25 mm from Treak Cliff, Derbyshire, described by Parkinson (1952) as *Dielasma hastata* (J. de C. Sowerby), are in fact specimens of *B. saccula*, but the largest specimens in that study belong to *Beecheria*: see below. These seem to be the commonest two species at Treak Cliff and from similar 'reef' environments of Asbian age, where *Dielasma* s.s. species have not, as yet, been recognized. The latter are more typical of Permian rocks.

Genus *BEECHERIA* Hall & Clarke, 1894

TYPE SPECIES. *B. davidsoni* Hall & Clarke, 1893, from the Windsor Group of Nova Scotia, Canada.

REMARKS. This genus was first separated from *Dielasma* in the mistaken belief that it had no dental plates. Bell (1929), in his study of Windsor Group faunas, discovered dental plates in the type species and reassigned it to *Dielasma*. Stehli (1956) revived *Beecheria*, recognizing that the dorsal cardinalia, in particular the hinge plates, differed, but he did not use topotypic material and provided illustrations of the internal morphology which do not match that of *B. davidsoni* (see Campbell 1965). Although the lectotype (Chicago University Museum catalogue no. 12223-475) is relatively short at 15·6 mm long, other specimens are bigger and other *Beecheria* species reach over 50 mm in length. They are amongst the largest Carboniferous terebratulids.

Beecheria species have not been recorded commonly from western Europe. However, inspection of our commonly quoted British terebratulid, *Terebratula hastata* J. de C. Sowerby, reveals that it belongs to *Beecheria*, and that other similar species also belong in this genus.

Beecheria is elongate in outline, with a somewhat flattened dorsal valve, when seen in profile. The anterior shell outline is rounded to emarginate, and the commissure is rectimarginate. Internally the ventral umbo has dental plates and in the dorsal valve the inner and outer hinge plates form a pair of V-shaped structures, widening onto the valve floor (Fig. 1F). Thus the inner socket ridges and outer hinge plates separate, and the median edges of the inner hinge plates also separate anteriorly on the valve floor. In this median space there is a delicate shelly platform barely separated from the valve floor (Fig. 15), which in life probably accommodated the ends of muscles.

Beecheria species include *B. hastata* (see below), a new species to be based upon specimens from Ireland and Derbyshire, specimens named as *Dielasma tumidum* by de Koninck (1887) from Belgium, and several species described by Weller (1914) from the Mississippi valley of the U.S.A. These range through much of the Viséan, but they are, perhaps, commonest in early to mid-Viséan strata.

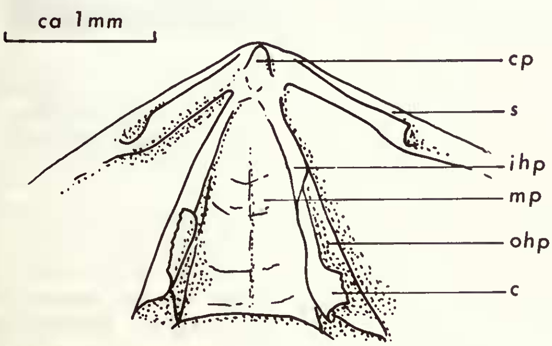


Fig. 15 Drawing of the posterior region of the dorsal valve interior of a silicified specimen of *Beecheria* from Ireland. Adult specimens have a weakly differentiated cardinal process (cp). The sockets (s) are widely separated from the outer and inner hinge plates (ohp, ihp) which form inverted V-shaped structures on the valve floor, well seen in sections (see Fig. 1F). The crural bases extend from the outer hinge plates as increasingly high ridges until, anteriorly, the crura (c) curve away ventrally. Medially, between the inner hinge plates, there is a slightly raised median platform (mp) of shell supported by a median ridge.

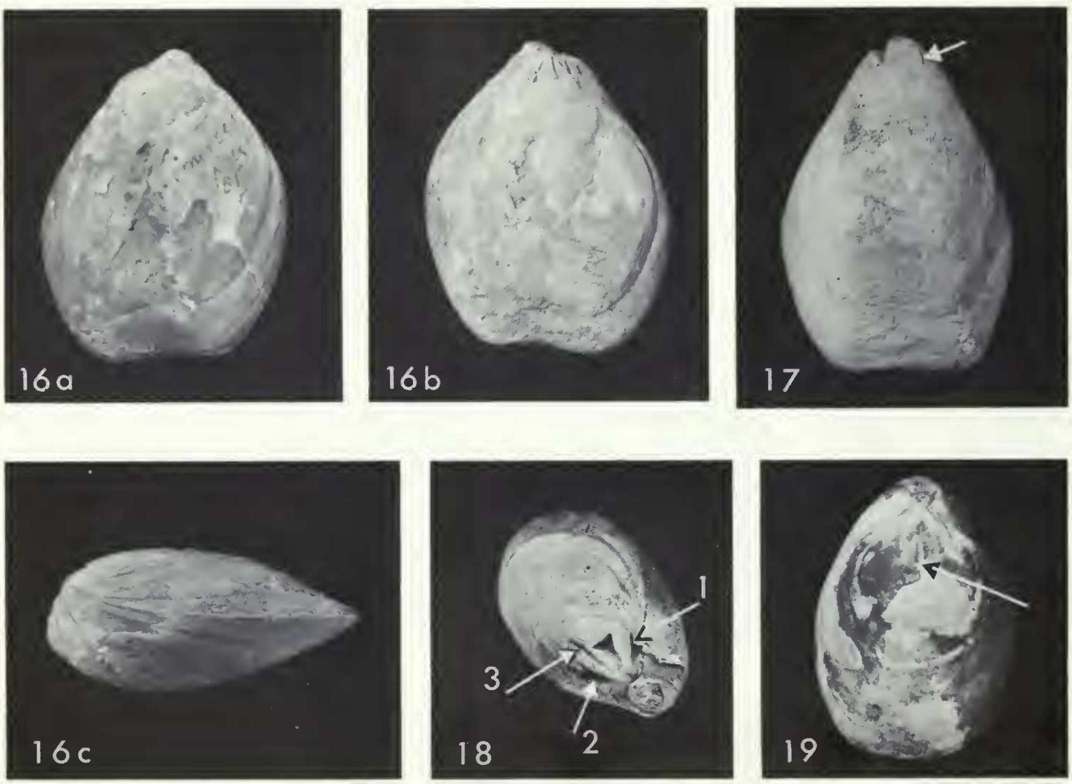
Beecheria hastata (J. de C. Sowerby, 1824)
Figs 16, 17

v* 1824 *Terebratula hastata* J. de C. Sowerby: 66; pl. 446, figs 2, 3.
p. 1858 *T. hastata* Sowerby; Davidson: 11; pl. 1, figs 1–3. 12.

Diagnosis. Large (reaching 40 to 50 mm long) ovate *Beecheria* with straight to emarginate anterior margin, commissure rectimarginate. Ventral valve with shallow, flat-floored sulcus from about 25 mm length to anterior; there may be a slight dorsal valve anterior sulcation.

Type specimen. *Terebratula hastata*, BM(NH) Palaeont. Dept. no. B 61657, figured by Sowerby (1824) in the centre of his pl. 446; presented to him by Mr S. Wright. Parkinson (1952), informally by inference, selected this specimen as lectotype (Fig. 16a–c).

Locality and horizon. Sowerby's locality is Limerick, Ireland, the exact locality being unknown. Douglas (1909), writing of *Dielasma hastata* from County Clare, said 'Sowerby's



Figs 16, 17 *Beecheria hastata* (J. de C. Sowerby). Fig. 16a–c, lectotype (sel. Parkinson, 1952), viewed ventrally, dorsally and laterally; from the Sowerby collection, Limerick, Ireland; of early Viséan age. BM(NH) Pal. Dept. no. B 61657, × 1. Fig. 17, ventral view of a specimen, also from Limerick, showing the positions of the dental plates (arrowed); this was sectioned serially to produce Fig. 20. BM(NH) no. B 81014, × 1.

Figs 18, 19 *Beecheria* sp. from Treak Cliff, Castleton, Derbyshire; of late Viséan, Asbian age. Fig. 18, dorsoposterior view of an internal mould showing the positions of dental plates, inner socket ridges (arrow 1), the V-shaped hinge plates (arrow 2) and the median ridge (arrow 3) supporting the median platform. BM(NH) no. BD 3, × 1·5. Fig. 19, a specimen with some of its shell missing showing the appearance of the divergent inner hinge plates and the median platform. BM(NH) no. BD 1, × 1·5.

original type specimen . . . without doubt came from the *Syringothyris* Zone', i.e. that it is of early Viséan age.

REMARKS. The name *hastata* has been a 'sack' name for Carboniferous terebratulids for many decades, and for almost as long it has been assigned to *Dielasma* King, 1859. However, inspection of Sowerby's type specimen (B 61657), which has lost shell from the postero-median region of the dorsal valve, shows quite clearly that the hinge plates do not fuse with the valve floor as expected in *Dielasma*, but do so along four anteriorly diverging lines (Fig. 16b), as in the genus *Beecheria*. A specimen of *B. hastata* (B 81014, Fig. 17) from Limerick, externally very like the lectotype, has been sectioned serially, giving 66 sections in all. A selection of these sections have been digitized and, by means of a computer, plotted to produce accurate drawings of the internal structures (Fig. 20). These clearly demonstrate the

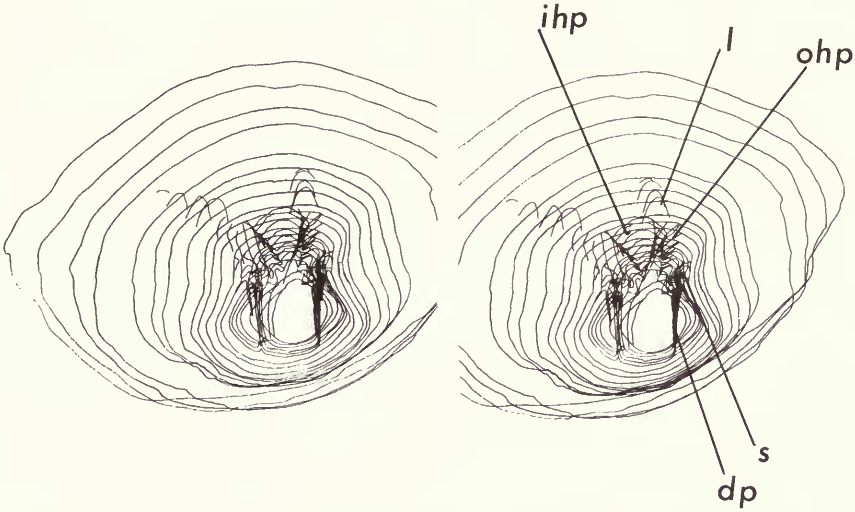


Fig. 20 *Beecheria hastata* (J. de C. Sowerby). Stereoscopic pair of drawings produced from a selection of 19 serial sections (from a total of 66) made from specimen B 81014 (Fig. 17). Each section was digitized and entered to a computer which controlled the plotting of the drawings, arranging them at the correct spacing and at the desired orientations. Use of a pocket stereoscope, with interocular distance of 60–65 mm, should provide full three-dimensional viewing. The posteriormost section was cut at 1·5 mm from the ventral umbo and the anteriormost, nearest, section at 24 mm from the umbo, beyond which point the loop was broken. The ventral valve is to the bottom, with clearly visible dental plates. Viewed posteriorly, into the umbo, tipped dorsally 20° and rotated 13° and 17° from the Z axis on the left and right drawings respectively, to produce an oblique view. ihp = inner hinge plate, l = posterior part of brachial loop, ohp = outer hinge plate, s = socket and dp = dental plate.

true *Beecheria* character of the cardinalia, including the thin elevated shelly material between the inner hinge plates, recorded also in the type species, *B. davidsoni* (see Fig. 18).

In the past the presence of dental plates in a Carboniferous terebratulid has commonly been sufficient evidence for calling it *Dielasma hastata*. Parkinson (1952), in his biometrical study of specimens misidentified as *D. hastata*, wrote of having specimens with dental plates 'sometimes preserved'. In fact his Treak Cliff, Derbyshire sample contained two common species, neither of which is *D. hastata*, pooled to give the presented results. The smaller, fatter individuals reaching about 22 mm long (commonly 16–18 mm long) are *Balanoconcha saccula*, while the thinner specimens with dental plates, reaching about 45 mm long, belong to a *Beecheria* species occurring also in County Fermanagh. This mixture of measurements from two species, one reaching about twice the length of the other, helps to account for the distinct break in slope of 'growth constants' which, as Parkinson (1960) later commented, manifested itself 'by a sudden increase in growth of the length and a temporary cessation of growth in the thickness of the shell'. Below the break specimens are a mixture of the two species, but mostly *B. saccula*; above the break all specimens belong to *Beecheria*.

Conclusions

The genus *Dielasma* King, 1859, is based on the Permian species *D. elongatus* (von Schlotheim). Other well-authenticated species of *Dielasma*, based on internal morphology, are also largely restricted to the Permian. Species of British terebratulids previously attributed to *Dielasma* prove, on studying their interiors, to belong to several genera, in particular to *Beecheria* and *Cryptonella*. Other species, usually of smaller sizes and with sulcate valves, belong to *Balanoconcha*, *Girtyella*, *Alwynia* and *Harttella*. Of these six genera only *Alwynia* had previously been recorded from Britain with certainty. Other than the eastern Australian *Balanoconcha*, the remaining four genera were all described from North American faunas. Despite this wide geographical spread, the ages of species in these genera are broadly comparable, with the exception that *Cryptonella* is recorded throughout the Upper Palaeozoic.

The importance of internal morphology in determining these terebratulids is stressed and these morphologies are believed to be expressed more meaningfully in the classification of Dagys (1972) than in that by Stehli (1965) in the *Treatise*. The presence of hinge plates, which accommodated pedicle adjustor muscles, and the natures of the pedicle apertures in these genera indicate the presence in life of inert pedicles (Richardson 1981) which kept the shell off the substrate but allowed its movement around the pedicle. In Recent terebratulids such pedicles are commonly divided into 'rootlets' at the distal end, allowing attachment to a wide variety of substrates, and the movement around the pedicle allows reorientation in varying water currents to achieve the most advantageous flow through the brachial cavity.

The diversity of six British Dinantian genera, so far recognized, contrasts with twelve Recent genera around the British Isles or seventeen from the Caribbean seas.

References

Bell, W. A. 1929. Horton–Windsor District, Nova Scotia. *Mem. geol. Surv. Brch Canada*, Ottawa, **155** : 1–268, pls 1–36.

Brunton, C. H. C. 1966. Silicified productids from the Viséan of County Fermanagh. *Bull. Br. Mus. nat. Hist.* (Geol.) **12** (5) : 171–241, pls 1–19.

—— 1968. Silicified brachiopods from the Viséan of County Fermanagh. *Bull. Br. Mus. nat. Hist.* (Geol.) **16** (1) : 1–70, pls 1–9.

Campbell, K. S. W. 1965. Australian Permian Terebratulids. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, Melbourne, **68**. vi + 113 pp., 17 pls.

Cloud, P. E. 1942. Terebratuloid brachiopoda of the Silurian and Devonian. *Spec. Pap. geol. Soc. Am.*, New York, **38** : 1–182, pls 1–26.

Cooper, G. A. & Grant, R. E. 1976. Permian brachiopods of West Texas, V. *Smithson. Contr. Paleobiol.*, Washington, **24** : 2609–3159, pls 663–780.

Dagys, A. S. 1972. [Postembryonic development of the brachidium of late Palaeozoic and early Mesozoic Terebratulida]. *Trudy̅ Inst. Geol. Geofiz. sib. Otd.*, Novosibirsk, **112** : 22–58, 28 figs. [In Russian].

Davidson, T. 1858 ('1857'). A Monograph of British Carboniferous Brachiopoda **2** (5, 1) : 1–48, pls 1–8. *Palaeontogr. Soc.* (*Monogr.*), London.

Douglas, J. A. 1909. The Carboniferous Limestone of County Clare (Ireland). *Q. Jl geol. Soc. Lond.* **65** : 538–586, pls 26–27.

Foster, M. W. 1974. Recent Antarctic and Subarctic brachiopods. *Antarctic Res. Ser. Washington* **21** : 1–189, 25 pls.

Koninck, L. G. de 1851. Supplément, *in: Description des animaux fossiles qui se trouvent dans le terrain Carbonifère de Belgique*: 651–716, pls 56–60. Liège.

—— 1887. Faune du Calcaire Carbonifère de la Belgique. *Annls Mus. r. Hist. nat. belg.*, Brussels, **14** : 1–154, pls 1–37.

Jansa, L. F., Mamet, B. & Roux, A. 1978. Viséan limestones from the Newfoundland shelf. *Can. J. Earth Sci.*, Ottawa, **15** (9) : 1422–1436, pls 1–2.

Matthews, S. C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology*, London, **16** (4) : 713–719.

Muir-Wood, H. M. 1951. The Brachiopoda of Martin's 'Petrificata Derbiensia'. *Ann. Mag. nat. Hist.*, London, (12) **4** : 97–118, pls 3–6.

Parkinson, D. 1952. Allometric growth in *Dielasma hastata* from Treak Cliff, Derbyshire. *Geol. Mag.*, London, **89** : 201–216.

—— 1960. Differential growth in Carboniferous Brachiopoda. *Proc. Geol. Ass.*, London, **71** (4) : 402–428.

Richardson, J. R. 1981. Brachiopods and pedicles. *Paleobiol.*, Lancaster, 7 (1) : 87–95.

Roberts, J. 1975. Early Carboniferous brachiopod zones of eastern Australia. *J. geol. Soc. Aust.*, Adelaide, **22** (1) : 1–32.

Sowerby, J. de C. 1823–25. *The Mineral Conchology of Great Britain*, **5**. 171 pp., pls 408–503. London.

Stehli, F. 1956. *Dielasma* and its external homeomorph *Beecheria*. *J. Paleont.*, Menasha, **30** (2) : 299–302, pl. 40.

—— 1961. New genera of Upper Palaeozoic terebratuloids. *J. Paleont.*, Menasha, **35** (3) : 457–466, pl. 62.

—— 1965. Paleozoic Terebratulida. *In* Williams, A. *et al.*, Brachiopoda **2** : H730–H762. *In* Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, **H.** 927 pp., 746 figs (2 vols), Lawrence, Kansas.

Weller, S. 1911. Genera of Mississippian loop-bearing Brachiopoda. *J. Geol.*, Chicago, **14** : 439–448.

—— 1914. The Mississippian Brachiopoda of the Mississippi Valley Basin. *Monogr. geol. Surv. Ill.*, Urbana, **1**. 508 pp., 83 pls.